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HOMOLOGY OF THE BODY SETÆ OF SOME LEPIDOPTEROUS LARVÆ.

By Y. HSUWEN TSOU.

I. INTRODUCTION.

The problem of homologizing the body setæ of lepidopterous larvæ has resulted from an attempt to name the body setæ of noctuid larvæ. In order to establish a nomenclature the writer was led to investigate whether or not, (1) the setæ on every body segment of any lepidopterous larva were serially homologous and (2) whether or not the setæ on every corresponding segment of every lepidopterous larva were homologous to each other. Due to a number of limitations it has not been possible to make an extensive study and it has not been possible to present all the forms studied. While the types treated do not cover the order Lepidoptera as a whole, yet it is believed that they will give a fair representation of the conditions found within it.

There are a number of difficulties in homologizing the body setæ of lepidopterous larvæ. First, there are no definite sclerites on any of the body segments. Second, some previous authors have conceived the body segments as divisible into annulets. Such a division of body segments, as will be shown later leads very frequently to a misinterpretation of the homology of setæ. In the mind of the writer even the position of the line of separation between the prothorax and the mesothorax is a debatable point. Third, the homology of the setæ can not be determined by their external structure, as the setæ in general show no differences from each other in their external appearance. In certain special cases, the setæ are plumose, spiny, clavate, or of some form divergent from the usual conditions, yet the obviously homologous setæ do not necessarily have the same structure. Fourth, the size of the setæ, in certain instances, can be employed as an aid, yet may be misleading. Fifth, the number and arrangement of the setæ of the

different segments have been modified more or less even in an individual larva, and also in larvæ of different species. In spite of all these points mentioned above the task of homologizing the body setæ has been undertaken, an attempt being made to sort out the corresponding setæ from a number of modifications in their form, number and location.

To determine the position of a seta on the segment of a larva is like indicating the position of a point on a plane surface. Two terms are always necessary for the precise statement of the position of any point on a surface. The position of a seta can not be determined without considering both its longitudinal and its transverse relations to the limits of the segment, mesal lines of the body and position of other setæ and of other structures of the segment.

Since the corresponding position of one seta with another is the only reliable means of homologizing the setæ of lepidopterous larvæ, then any seta of one segment, can not be homologized in a strict sense, with any set of another segment, unless the former has both a similar longitudinal and a similar transverse relation to other structures with the latter, because both of these relations are equally important.

The segments of a larva vary to a certain extent in width and very greatly in length. The corresponding segments of different species differ in absolute size and also slightly in relative size. Therefore, the position of a seta on a segment is stated proportionally with reference to other setæ on the same segment.

Recalling all the difficulties mentioned above, one would naturally think that homologous setæ might not correspond with each other in the positions they occupy on different segments of any particular species, or on the corresponding segments of different species, or that they might be similar only in one of their longitudinal or transverse relations to other structures. The homology of the setæ determined in this paper is not, in any sense, based upon such an assumption, and any discrepancy regarding the positions which the homologous setæ occupy should be satisfactorily explained. Illustrations may be found in a single species by studying its different segments; while in the case of different species it will

be found by studying the corresponding segments, because, in the former, changes that have taken place in different species may not have taken place in the particular species concerned; and in the latter case, those that have taken place in other segments may not occur in a particular segment. The homologies, in most cases, are not copied from previous authors. The writer does not venture to disbelieve the studies that have been recorded in this field, but is afraid of misinterpreting their meaning.

Guarded by such restrictions both the selective and eliminative methods are frequently employed. The selective method is to select on the segments concerned an obviously homologous seta, or a group of setæ, for a starting point. The conception of the homology of this single seta, or group of setæ, should be retained if proved by studying the other setæ of the same segments, and rejected if disproved. The eliminative method is to eliminate the setæ whose homology has been already determined. Those which remain on one segment may not necessarily be homologous with the ones remaining on another segment. Therefore, any rejection of their homology should be also satisfactorily explained.

The setæ, as we know, vary in size, number and arrangement. The number and location of setæ can not be individually precisely ascertained without detailed careful microscopic examination. After these are ascertained, a comparative consideration of the relation which a certain seta or a group of setæ bears to the other setæ of the segment concerned must be made. A comparative consideration of the setæ of the segment being studied as a whole with the setæ of the same and different segments, of the same and different larvæ, must also be carried on before the arrangement of the setæ on the segment under consideration can be thoroughly understood. These methods of examination and consideration are indispensable and supplement each other. The results obtained by successively employing these methods will on the one hand neglect no minor points, and on the other hand lay no undue emphasis on certain peculiarities.

With the above procedure, the sections on the study of the different segments of the same larva and the study of the same segments of the different larvæ are written. These two studies

are isolated representations of facts, but not theories; and as independent studies serve as a check upon each other. A general discussion follows for the purpose of correlating the results obtained. The results are to be retained if in harmony, rejected if they are not. It is in this section on general discussion that doubtful points are discussed and quotations and theories are cited.

The body setæ of lepidopterous larvæ have been designated hitherto by numbers. Different authors have not employed the numbers in the same way. The homologies here proposed are unlike any of those previously proposed. The writer finds it necessary to employ a nomenclature of his own. The setæ are divided into groups: as anterior (A), dorsal (D), subdorsal (S), circumstigmatal (C), lateroventral (L), pseudopodal (P), and mid-ventral (M). Each group of setæ is designated with the capital initial letter of the name of the group; as A, D, etc. Each individual seta of the group is numbered as D_1 , P_4 , etc., or sub-numbered as A_{1a} . The setæ belonging to the above groups are regarded as primary setæ. The setæ found on certain larvæ and not included in the above groups are designated as additional (ad), and numbered ad_1 . The promiscuous setæ found on certain caterpillars are regarded as secondary and are not named. When a single primary seta, or a group of setæ, is represented by a cluster of setæ, this primary seta, or this group of primary setæ, is considered as tufted. When a cluster consists of one or more setæ in addition to its usual number of setæ, it is considered as a tuft. A primary seta, or a group of setæ, or a tuft of setæ is termed warted if it is borne upon an elevated portion of the integument. The groups of setæ here designated are more or less artificial in character, but are decidedly advantageous for the purpose of designating the coalesced tufts, and the reduction or the addition in the number of setæ within a group, and also in meeting some minor difficulties resulting from the study of the same and different segments of larvæ.

Practically all the materials used in this study were inflated and determined specimens purchased through the agency of the American Entomological Company, Brooklyn, New York. The inflated specimens are very easily broken in handling and it has

been found convenient not only to examine but also to preserve the specimens in alcohol. This method prevents breakage and it is then possible by the aid of the microscope to detect the presence and to determine the number of extremely small setæ.

In this paper there are a number of diagrammatic sketches, indicating the relative positions of the setæ, which are termed setal maps. One-half of the segment only is represented on each setal map. The relative position of the setæ on the convex surface of the body segment are retained as closely as possible on the flat surface of the setal maps. On the setal maps only the position of the base of the thoracic legs is indicated. The boundary of the cervical shield is indicated whenever it is not too indefinite to be traced out. The positions of the other strongly chitinated portions of the integument and the positions of the punctures are usually not indicated.

The different segments of any larva are not of the same length and breadth. The same segments of different larvæ vary slightly in the ratio of their length and width. In order to secure a uniformity for purposes of comparison a larva was selected in which there was an average ratio of the length and width of every segment. The larva selected was slit along one side and the skin was mounted flat on a slide. The dimensions of each segment were taken as the average ratio of the same segments of other larvæ for the ratio of the dimensions of the setal maps. The setal maps are of the same size for the same segments of different species, but not of the same size for the different segments of the same larva. The sizes of the setal maps of the different segments of the same larva were made to a uniform width.

The setal maps are similar to geographical maps in the character of having only four directions, cephalic, caudal, dorsal and ventral, since every larva is generally cylindrical and without longitudinal sutures on every segment. In describing the location of setæ the writer has found it convenient to recognize only the four directions which are common to a setal map. This specification of directions holds true only in locating the setæ, not in describing other structures.

The phrase "in line" is very frequently employed. A few

words of explanation are necessary. If the directions of a line are not stated, the phrase "in line" always refers to a straight line joining two or more points which are either parallel with or perpendicular to the dorso-mesal line.

The writer wishes to express his gratitude first of all to Dr. A. D. MacGillivray* whose sympathetic and devoted attention has alone made this study possible. Mr. S. B. Fracker, who made a study of the homology of body setæ of lepidopterous larvæ, using some of the writer's specimens after the writer's conclusions had been practically formulated, has pointed out a number of differences between the homologies proposed in this paper and those previously proposed. Mr. J. R. Malloch has read this paper and verified some of the expressions. Mr. Z. C. Dage has aided the writer in making the drawings. To each and to all of the above the writer is very much indebted.

II. A STUDY OF THE DIFFERENT SEGMENTS OF THE SAME LARVA.

Every species in this section is treated separately without seeking any explanation of the homology of the setæ beyond the particular species concerned. The mere repetition of statements is in most cases avoided. In each species treated the prothorax is always the starting point and the segments caudad of the prothorax are studied successively. In the usual practice of homologizing structures a generalized condition of structure is taken for a starting point, but such is not the case here. If one starts with such an assumption he is in the danger of being misled.

The prothorax is chosen simply because it is the most cephalic segment of the body, and not because of any assumption regarding its degree of generalization. The prothorax is described for the purpose of finding the exact number of setæ present on this segment and of stating the relative position of each seta. To homologize the mesothoracic setæ with the prothoracic setæ an effort has been made to find every seta upon the mesothorax, compare it with the prothoracic setæ, and then to determine its homology by considering both its transverse and longitudinal relations to other

*Although the work upon which this paper is based was done under the direction of Dr. MacGillivray as instructor, the writer must assume the responsibility for its general conclusions, with some of which Dr. MacGillivray is not in accord.

structures. To homologize the metathoracic setæ with the mesothoracic setæ a similar method of procedure is followed.

(a) *Hepialus humuli* L.

Description of prothorax. On the caudal two-thirds of the dorsal half of the prothorax there is a more strongly chitinized portion of the integument which has been termed the cervical shield by previous authors. On the cervical shield, there are nine setæ of different sizes. These nine setæ are designated by the following characters: A_1 , A_2 , D_1 , D_2 , S_1 , S_2 , C_1 , C_2 , C_3 . As a matter of convenience these nine setæ may be divided into two rows or two groups: D_1 , A_1 , A_2 , S_2 and C_3 constitute the cephalic transverse row or group. D_2 , S_1 , C_1 , and C_2 constitute the caudal transverse row or group. D_1 is the dorsal seta of the cephalic group. A_1 is slightly caudad of D_1 and at an equal distance between D_1 and A_2 . The distance between S_2 and A_2 is shorter than the distance between A_2 and A_1 . C_3 is ventrad and a trifle caudad of S_2 . The distance between C_3 and S_2 is shorter than the distance between S_2 and A_2 . Of the caudal group of four setæ S_1 and C_1 are in line and are the cephalic setæ of the caudal group; D_2 is caudo-dorsad of S_1 , and C_2 is caudo-ventrad of C_1 . The relative position of the setæ of one row to that of the other row may be noticed. S_1 is between A_1 and A_2 , C_1 between A_2 and S_2 , C_3 is the ventral seta of the cephalic row, and C_2 of the caudal row. They are both about in line with the ventral third of the thoracic spiracle.

As a matter of convenience the setæ on the cervical shield can also be subdivided into dorsal and ventral groups instead of cephalic and caudal groups. S_2 , C_1 , C_2 and C_3 constitute the ventral group, and the remainder of the setæ, the dorsal group. It should be emphasized in this connection that such groups or rows are purely artificial conceptions employed for facilitating the task of description and should not be considered, in this place, at least, as having anything to do with the primitive arrangement of the setæ.

Regarding the size of the setæ it may be mentioned that D_2 and C_1 are the smallest of the nine setæ on the cervical shield, and both of these are encircled at the base by a black ring. D_1 and C_2 are next in size, and all the others are larger than D_1 and C_2 , and

subequal to each other. Besides the nine setæ, there are two punctures on the cervical shield. One is near to and dorso-caudad of A_1 , the other is near to and dorso-caudad of A_2 .

Ventrad of the cervical shield and immediately dorsad of the base of the leg, there are two setæ designated as L_1 and L_2 . These setæ are situated on a more strongly chitinized portion of the integument. Cephalad of the leg, there are four setæ designated as P_1 , P_2 , P_3 , and P_4 . These four setæ differ in size from each other but they are all minute. Caudad of the leg, there is a seta designated as M.

Homologizing the Mesothoracic Setæ with the Prothoracic Setæ. The mesothorax is longer and wider than the prothorax. The mesothoracic setæ are therefore more widely separated on that segment than those on the prothoracic segment. There is not a large, strongly chitinized portion of the mesothoracic integument which is comparable to the cervical shield of the prothorax. The strongly chitinized portions of the mesothoracic integument are rather small and separated. There is, however, a portion of the mesothoracic integument which bears no setæ and which is wide enough to give the idea that it divides the mesothoracic setæ into a dorsal and a ventral region. A line drawn across the mesothorax from the ventral margin of the thoracic spiracle parallel with the dorso-meson will mark the ventral limit of the dorsal region.

The homology of the setæ of the ventral region of the mesothorax can be readily determined. The single seta caudad of the mesothoracic leg is in a corresponding position with the prothoracic M, and the group of four minute setæ cephalad of the mesothoracic leg is in a corresponding position with prothoracic P as a group. Therefore, these setæ of the mesothorax are M and P respectively. Each of the four minute setæ within the group of mesothoracic P finds its proper homologous seta within the group of prothoracic P on account of the fact that the former corresponds relatively in position and is similar in size with the latter.

The differences between these four setæ cephalad of the legs of these two segments are that the setæ of mesothoracic P as a

group are larger than the prothoracic P, and the individual setæ among the mesothoracic P are more widely separated. Without considering the setæ of these segments in general, the only remaining seta of the ventral region of the mesothorax may be labeled L_2 , as it corresponds exactly in position with the prothoracic L_2 . The prothoracic L_1 has no homologous seta on the mesothorax. It can not be homologized with any seta of the ventral region of the mesothorax because all these setæ have their homology precisely determined, and there is no remaining seta in the ventral region; nor can it be homologized with any seta on the dorsal region because of its position. Since L_1 and L_2 of the prothorax are very close to each other in position, it is safer to call this seta of the mesothorax L instead of L_2 , because it is difficult to say which L is retained and which lost.

In the dorsal region of the mesothorax there are seven large setæ and four minute setæ. These four minute setæ are on a somewhat elevated, more strongly chitinized portion of the integument, and are the most cephalic setæ of the dorsal region. On the cervical shield of the prothorax, as previously described, there are two rows of setæ, and there are four setæ in the caudal row. On the mesothorax the four caudal setæ form a row, although they are more widely placed than those of the prothorax. The general appearance of a row is, however, retained on the mesothorax and also the two middle setæ of these four are in line and cephalad of the other two. As they correspond in position to those of the prothorax, these four setæ of the mesothorax can be safely and respectively designated as similar to those of the prothorax, D_2 , S_1 , C_1 , and C_2 .

D_1 is the dorsal seta of the cervical shield of the prothorax, and in a corresponding position on the mesothorax, there is also a single seta which may be homologized with D_1 . There are two setæ on the prothorax in line with D_1 , namely A_2 and S_2 , while in line with D_1 of the mesothorax there is only one seta, yet unnamed.

The distance between D_1 of the mesothorax and the seta yet unnamed is greater than the distance from D_1 to A_2 of the prothorax and a little less than D_1 and S_2 of the prothorax. The seta yet unnamed is designated as S_2 and the reason of this designation

will be understood when the homologies of the other setæ are all determined. Ventrad of S_2 of the prothorax there is only one seta, C_3 , while ventrad of the S_2 of the mesothorax, there remains only one seta in the dorsal region. If we can only assume that the determination of the homology of the seta just named as S_2 is correct then this one remaining seta is without doubt C_3 . Now ventro-caudad of C_3 and nearer to it than the distance between S_2 and C_3 of the prothorax is a bar-like chitinized scar. What is the origin of this scar? If this scar is a seta, it ought to be circular instead of bar-like. If we disregard this bar-like scar then the homology of S_2 and C_3 is clearly beyond doubt. The remaining setæ in the dorsal region of the mesothorax are on a wart which bears four small setæ. No such wart or setæ are on the prothorax cephalad of the cervical shield. If these two pairs of setæ can be homologized at all, the dorsal pair is A_1 and the ventral pair A_2 , as they are in a similar position with the prothoracic A_1 and A_2 .

The homology of the setæ in the dorsal region of the mesothorax is determined thus far by arranging and studying them as cephalic and caudal groups. The result thus far obtained may be checked by means of arranging the same mesothoracic setæ and studying them as dorsal and ventral groups. Thus, S_2 , C_1 , C_2 and C_3 of the prothorax may be regarded as a group, while S_2 , C_1 , C_2 and C_3 of the mesothorax may be also regarded as a group. They are in corresponding positions so they must be homologous. D_1 and S_1 of both the prothorax and mesothorax are in corresponding positions, then the remaining caudal one must be homologous with D_2 , and the two pairs of setæ on the wart must be homologous with A_1 and A_2 respectively.

The structures remaining are two punctures of the prothorax which find no homology in the mesothorax, and the bar-like scar of the mesothorax which finds no homology in the prothorax.

Comparing the mesothorax with the metathorax there is not a great amount of difference between them. Yet slight changes can be pointed out. The distance between C_1 and C_2 is shorter on the metathorax than on the mesothorax; and A_1 and A_2

are not on a wart, but on a common chitinized portion of the integument of the metathorax.

Homologizing the First Abdominal Setæ with the Metathoracic Setæ. When the metathorax is compared with the first abdominal segment the more striking differences are that the first abdominal segment is without either a leg or a proleg and has in addition a spiracle. Because of these features one would naturally expect that the arrangement of setæ would be modified.

The prolongation of the line marking the ventral limit of the dorsal region of the mesothorax will also divide the first abdominal segment into two regions. The regions thus designated are for convenience only. The metathoracic D_1 , D_2 , S_1 , C_1 , C_2 , C_3 find their homologous setæ corresponding exactly in positions on the dorsal region of the first abdominal segment. In the corresponding positions of the metathoracic A_1 and A_2 there is on the first abdominal segment only one minute seta which can be designated as A . There remains only a single seta yet unnamed. If it can be homologized at all, it should be S_2 . If this is the only reason for such an homology one may hesitate to call the remaining seta S_2 . The cephalo-caudal distance between the setæ of the first abdominal segment, however, is much less than that between the setæ of the metathorax. Regarding the homology of D_1 and D_2 of the first abdominal segment there is no doubt. The distance between D_1 and D_2 of the first abdominal segment is much shorter than that of metathorax. Furthermore, S_2 is in line with D_1 throughout all the thoracic segments and this remaining seta just determined as S_2 of the first abdominal segment is also in line with D_1 of the same segment. Therefore, this remaining seta can be safely designated as S_2 .

On the ventral region of the first abdominal segment there is no leg and the number of setæ is equal to that of the ventral region of the metathorax. The ventral seta of the ventral region can be very easily determined as homologous with M of the metathorax. The group of four setæ cephalo-dorsad of M of the first abdominal segment can be homologized with the metathoracic P . The objection to this homology is that the group of four setæ just determined as the first abdominal P is much nearer to the first

abdominal M than the metathoracic P is to the metathoracic M. This objection can be very easily removed by the fact that from the study of the dorsal region of the first abdominal segment, the approximation of the setæ along the cephalo-caudal direction is obvious. So this group of four setæ can be homologized with P_1 , P_2 , P_3 and P_4 of the metathorax respectively. There remains only one seta on the first abdominal segment to be homologized. L of the metathorax is in a position between the first abdominal P_2 and the only remaining seta. Judging from such a relative position, L of the metathorax can be homologized with either of these two first abdominal setæ. Since the homology of P is decided, L of the metathorax must be homologous with this remaining seta of the first abdominal segment.

The difference in the size between the homologous setæ of the metathorax and those of the first abdominal segment should be noticed. S_1 of the first abdominal segment is much smaller than S_1 of the metathorax. The setæ of P of the first abdominal segment as a group are larger than the metathoracic P as a group, yet the relative proportion of size is retained within the group, e. g., P_4 remains the smallest one of this group.

Homologizing the Second Abdominal Setæ with the First Abdominal Setæ, and so forth to the Eighth Abdominal Segment. The homology of the setæ of the first eight abdominal segments is very obvious and unmistakable. Therefore, only the features of striking difference will be noted as follows: P_4 of the second abdominal segment is larger than P_4 of the first abdominal segment. P_4 of the second abdominal segment is also nearer to P_3 of the second abdominal segment, than the distance between P_4 and P_3 of the first abdominal segment. On the third, fourth, fifth and six abdominal segments where the prolegs are present, P as a group is on the side of the proleg. P_3 is absent in the seventh abdominal segment. On the seventh abdominal segment, P_4 is more distant from P_1 and P_2 , considering their cephalo-caudal direction. P_4 on the eighth abdominal segment is smaller than P_4 on the preceding segment. S_2 gradually diminishes in size from the caudal segments, and L is smallest on the eighth abdominal segment. C_2 and C_3 gradually depart in a cephalo-caudal direc-

tion from the spiracle until the sixth abdominal segment is reached. On the seventh and eighth abdominal segments^{245834hrdtamhtamt} much nearer to the spiracle than on the previous segments. Regarding a cephalo-caudal direction, the distance between C_2 and C_3 of the eighth abdominal segment is shorter than the distance between C_2 and C_3 of the preceding abdominal segments.

Homologizing the Ninth Abdominal Setæ with the Eighth Abdominal Setæ. The setæ on the ninth abdominal segment, although they differ in number and arrangement from the setæ on previous segments, can be easily homologized by comparing them with the setæ on the eighth abdominal segment. On the ninth abdominal segment, C_1 is nearer to C_2 and C_3 is nearer to L than they are on the eighth abdominal segment; P_4 is smaller than it is on the eighth abdominal segment, but is in exactly the same position, and it is proportional in size with the P_4 on the eighth abdominal segment. The absence of S_2 is determined from the fact that S_2 of the eighth abdominal segment is small and corresponds to no seta on the ninth abdominal segment in this position.

The Setæ on the Anal Segment. The setæ on the anal segment differ very much in number and arrangement from the setæ on all the other body segments. The writer considers the anal segment to consist of more than one segment and believes the homology of the setæ of the anal segment can be determined by comparing them with the setæ of the ninth abdominal segment.

(b) *Cossus cossus* L.

Description of Prothorax. On the prothorax there is a cervical shield which extends ventrad into the dorsal one-third of the prothorax. There are six setæ on the cervical shield, three in a cephalic row and three in a caudal row. These are respectively designated as A_1 , A_2 , D_1 , D_2 , S_1 and S_2 . Near the middle of the prothorax and cephalad of the thoracic spiracle there are two setæ which are designated as L_1 and L_2 . In front of the prothoracic leg there is a group of three setæ which are designated as C_1 , C_2 and C_3 . Above the base of the prothoracic leg there is a group of three minute setæ, which can not be seen without high magnification, and this group is designated as P ; and the individual setæ

of the group are designated respectively as P_1 , P_2 , P_3 . Caudo-ventrad of the leg there is a single seta, designated as M.

Homologizing the Mesothoracic Setæ with the Prothoracic Setæ. In the corresponding positions of C_1 , C_2 , C_3 of the prothorax there is also a group of three setæ on the mesothorax. These three setæ of the mesothorax as a group are undoubtedly homologous with C_1 , C_2 , and C_3 of the prothorax. Considering each one of the three setæ individually the proposition is somewhat different. On the mesothorax, although there is one seta caudad of two cephalic ones, yet the caudal one is dorsal in position and the ventral one of the two cephalic setæ is cephalic in position on the mesothorax, while they are in a reverse relation on the prothorax. The homology assigned to these three setæ individually is not so evident as when they are considered as a group.

The most dorsal seta of the mesothorax is homologous with D_1 of the prothorax, because both are equally distant from the dorso-meson, and also are similar in their longitudinal relations with other structures on their respective segments. For the same reasons mentioned above, the two setæ immediately ventrad of D_1 of the mesothorax can be homologized with D_2 and S_1 of the prothorax. The seta, ventrad and in line with D_1 , D_2 and S_1 of the mesothorax, corresponds with S_2 of the prothorax only in the distance from the dorso-meson. It is determined as S_2 of the mesothorax for two reasons. First, it corresponds more nearly to S_2 of the prothorax than to any other prothoracic seta. Second, S_2 in comparisons with all the other setæ of the thoracic segments has a thicker and blacker ring at the base. By means of their corresponding positions, prothoracic A_1 and A_2 can be homologized with the two cephalic pairs of minute setæ respectively. In this connection there are two questions. First, why A consists of two pairs of minute setæ on the mesothorax instead of two large single setæ as on the prothorax. Second, A_{1a} is too far cephalad and is apparently on the prothorax instead of the mesothorax. The answer to the first question is, that they can be homologized with nothing else, and further proof will be shown in a later section of this paper. The answer to the second question will be given in the discussion of the metathoracic setæ of this same larva.

The remaining setæ on the mesothorax are L, M and P, a group of four setæ. They are in corresponding positions with their homologous setæ on the prothorax.

Homologizing the Metathoracic Setæ with the Mesothoracic Setæ. All the metathoracic setæ except A_{1a} are very obviously homologous with all the mesothoracic setæ. In order to determine the homology of the single minute seta on the caudal margin of the cervical shield, the larval skin of a *Mamestra legitima* was mounted flat on a glass slide. The reason for using the larval skin of a *Mamestra legitima* is that whenever a careful search is made on any larva of the generalized *Frentæ*, a seta corresponding to the seta of *Cossus cossus* under consideration is found.

The larval skin of the *Mamestra legitima* was cleared for a few minutes in boiling 4% caustic potash in order that the sutures could be seen more plainly. After clearing, the larval skin was mounted on a glass slide with Canada balsam. Examining the slide under a microscope with transmitted light, no suture is apparent on the line of separation between the prothorax and mesothorax, but there is a suture (?) immediately cephalad of the minute seta at the caudal margin of the cervical shield. The writer was unable to trace the ventral extent of this suture, but he is sure that the ventral extension of the cervical shield is not limited by a suture. Therefore, as will be shown later, this suture can not even be considered as the suture limiting the cervical shield, but may be considered as the suture separating the prothorax and the mesothorax. One may think that this conclusion drawn from a very limited study is not valuable. We may seek some other evidences.

It is almost an established fact that no insect has a pair of prothoracic spiracles. Therefore, the first pair of spiracles of lepidopterous larvæ belongs morphologically to the mesothorax, while they are apparently situated on the prothorax. One may think that the migration of the spiracle may have nothing to do with the migration of setæ. But this case of close analogy opens a possibility that the mesothoracic seta may migrate considerably cephalad, and also proves that the apparent line of separation between the prothorax and the mesothorax is not the true line of separation between these two segments. Furthermore, if this

minute seta at the caudal margin of the cervical shield of *Cossus cossus*, which has been named as A_{1a} of the mesothorax, is not homologous with the metathoracic A_{1a} , it can not be homologous with anything else. It is for these reasons that the writer ventures to draw the conclusion that the minute seta at the caudal margin of the cervical shield of *Cossus cossus* belongs to the mesothorax and is named A_{1a} and considered homologous with the metathoracic A_{1a} .

Homologizing the First Abdominal Setæ with the Metathoracic Setæ. Two of the dorsal setæ of the first abdominal segment labeled D_1 and S_2 are based upon several facts. First, the relative distances between the dorso-mesal line and each of these two setæ are similar to the distance between the dorso-mesal line and each of the metathoracic D_1 and S_2 . Second, although these two setæ of the first abdominal segment are not midway between the cephalic and caudal limits of the segment as the metathoracic D_1 and S_2 are, yet they are not too far forward from the middle of the segment. Third, the relation of the first abdominal D_1 and S_2 is the same as the relation of the metathoracic D_1 with S_2 , as D_1 and S_2 of both segments are almost transversely in line. Between the metathoracic D_1 and S_2 and also in line with them there are two setæ, while in the case of the first abdominal D_1 and S_2 there are no setæ in line with them, but there is a single seta yet unnamed between the caudad of them. This seta may be either D_2 or S_1 . Judging from its transverse relation to the dorso-meson, it is homologous with D_2 of the metathorax. The homology of A, C_1 , P, M and L is very evident. The remaining two setæ can be nothing else than C_2 and C_3 . However, this is not the only ground for determining their homology. The homology of C_2 and C_3 is also demonstrable by the fact that the first abdominal C_2 and C_3 correspond somewhat in position with the metathoracic C_2 and C_3 . Based upon the fact that the prothoracic C_2 and C_3 are in line with the ventral margin of the thoracic spiracle while the first abdominal C_2 and C_3 are ventrad of the ventral margin of the first abdominal spiracle, one may doubt the conclusion just made on the homology of C_2 and C_3 of the first abdominal segment and of the metathorax. The answer to this is that the thoracic spiracle

is located more ventrad than the abdominal spiracle. Furthermore, it has been proven that the first abdominal setæ are homologous with the prothoracic setæ only indirectly through the metathorax, then the mesothorax, but not in a direct way.

Homologizing the Second Abdominal Setæ with the First Abdominal Setæ, and so forth to the Eighth Abdominal Segment. The homology of the setæ of the first eight abdominal segments is very obvious and needs no comment. Yet some striking features of difference among them may be noticed. D_1 and D_2 gradually approach each other to a dorso-ventral direction, and are longitudinally in line with each other on the eighth abdominal segment. The distance between S_2 and C_1 is variable. P_1 , P_2 and P_3 are situated on the side of the proleg when the proleg is present, P_4 is absent on the eighth abdominal segment.

Homologizing the Ninth Abdominal Setæ with the Eighth Abdominal Setæ. The homology of the ninth abdominal A_1 , A_2 , D_2 , C_1 , C_2 , C_3 , L , P_1 , P_2 , P_4 and M is easily determined. The homology of D_1 can be explained by the relative position with A_1 and the ventral migration on the preceding abdominal segments. Since the homology of all the setæ found on the ninth abdominal segment is determined then the absence of S_2 on the ninth abdominal segment is evident.

(c) *Jaspedia celsia* L.

Description of Prothorax. On the prothorax there is a cervical shield and on the cervical shield there are six setæ designated as A_1 , A_2 , D_1 , D_2 , S_1 and S_2 . Ventrad of the cervical shield there are two setæ on a common chitinized portion of the integument designated as C_2 and C_3 . Ventrad of these setæ and dorsad of the base of the leg, there are two setæ on a common chitinized portion of the integument which are designated as L_1 , L_2 . On the cephalic end of the ventro-mesal line there is an integumental projection. Dorsad of this projection and cephalad of the leg there are three setæ designated as P_1 , P_2 , and P_3 . Ventro-caudad of the leg is a single seta designated as M .

Homologizing Metathoracic Setæ with the Prothoracic Setæ. Judging from their longitudinal and transverse relations with each other and with the leg and mesal, cephalic and caudal limits of the

respective segments the homology of A_1 , A_2 , D_1 , D_2 , S_1 , S_2 , C_2 , C_3 , L , M , and P (as a group) is very evident. Since all those setæ above are determined, the remaining single seta can be nothing else than a seta which is not found on the prothorax of this particular larva. This seta of the mesothorax, yet unnamed, is designated as C_1 .

Homologizing the Metathoracic Setæ with the Mesothoracic Setæ. Although by means of actual measurement one can readily detect some slight differences in the relative positions of the methathoracic setæ and the mesothoracic setæ, yet their homology is very evident, except that of A_{1a} , which can be explained by the discussions previously given.

Homologizing the First Abdominal Setæ with the Metathoracic Setæ. Avoiding repetitions, there are only two setæ on the first abdominal segment that it is necessary to discuss—one caudad of the spiracle, and the other ventrad of the spiracle. The single seta caudad of the spiracle can be homologized, either with the metathoracic C_1 on account of the fact that they are very similar in both their longitudinal and transverse relations with the other structures on their respective segments, or with the metathoracic C_3 , because C_1 is the seta most liable to be absent, as has been the case on the prothorax. The single seta ventrad of the spiracle may be homologized with the metathoracic C_2 , because both are in very closely corresponding positions, or with C_3 , on account of the fact that C_2 of both the mesothorax and metathorax is small and most liable to be atrophied. These two setæ are without doubt two of the three C's, no matter whether the group C is a natural or an artificial one, but it is difficult to say which of the two C's they are. The precise determination of the homology of these two setæ will be stated in a later section of this paper.

Homologizing the Second Abdominal Setæ with the First Abdominal Setæ, and so forth to the Eighth Abdominal Segment. The homology of the setæ on the first eight abdominal segments is very obvious, yet a number of striking variations will be stated. D_1 and D_2 gradually approach each other in a dorso-ventral direction and become longitudinally in line with each other on the eighth abdominal segment. The relative positions between the spiracle

and the four setæ (A_2 , S_2 , C_2 and C_3) surrounding it vary with each segment. The most striking one among the four setæ is C_2 , which gradually fluctuates dorsad or ventrad on the first six segments and abruptly ventrad on the seventh and then abruptly dorsad again on the eighth segment. L migrates slightly cephalad or caudad on the first six segments and abruptly cephalad and in line with C_3 on the seventh, and abruptly caudad again on the eighth segment. P_1 , P_2 , and P_3 are on the side of the proleg when the proleg is present. P_2 disappears on the seventh segment, and P_3 on the eighth.

Homologizing the Ninth Abdominal Setæ with the Eighth Abdominal Setæ. The only seta which requires discussion is the most cephalic minute seta of the dorsal fourth. It is best to call it A , because it can be either A_1 , or A_2 .

The writer presents his study of only three species in this section since he was limited by time and also to avoid repetitions. These three species treated above cover only in part the types of arrangement of the body setæ of lepidopterous larvæ, but furnish a sample of treatment which is considered to be the proper method for determining the homology of the setæ of any species of larva.

The reader may notice that when the selective method was employed, the selection was always the right one. The writer purposely avoided the discussion of a wrong selection. An example, however, may be sought in homologizing the first abdominal setæ of *Hepialus humuli* with the metathoracic set of the same. One may assume the metathoracic L to be one of the P 's of the first abdominal segment because it can be either one of the P 's or the seta immediately ventrad of the spiracle. As one proceeds to determine the other setæ ventrad of this seta whose homology he has just assumed, he will find his assumption false, unless he overlooks one seta or discards one seta unreasonably.

It is not the proposed plan to summarize the results obtained from the foregoing studies in this section. There is one thing which, however, should be emphasized, and that is, that the homologous setæ of all the different segments of the same larva can never be joined by a perfectly straight line. This is due to the fact that the setæ change their positions in certain cases and the segments are not of the same width throughout. Therefore it was considered a safeguard against errors to homologize the setæ of each following segment only with its immediately preceding segment.

III. THE STUDY OF THE SAME SEGMENTS OF DIFFERENT LARVÆ.

Since the setal arrangement of the body segments of lepidopterous larvæ does not differ in every segment, but in groups of

segments, the body segments are divided according to their setal arrangement into four groups: (1) the prothorax, (2) the mesothorax and metathorax, (3) first eight abdominal segments, (4) the ninth abdominal segment, and (5) the anal segment.

Judging from the presence of scales alone one could rank thysanurous insects with the order Lepidoptera. So the resemblance of certain special characters furnishes no clue to the phylogeny of the owner. This is the greatest difficulty which one will meet with in homologizing the larval setæ by the study of the same segment of different larvæ. Aside from the restriction of using no evidences of the segments other than the segments under consideration the writer restricts himself in homologizing the setæ of *Cossus cossus* with that of *Hepialus humuli*; no evidence from any larva other than these two species will be quoted. The reasons for making this restriction are that: (1) *Hepialus* belongs to a separate suborder, the Jugatæ; and (2) *Cossus cossus* is one of the most generalized Frenatæ so far as wing venation is concerned. By such a restriction one may not be confused by some special characters to misinterpret the homology. Different larvæ vary in size, and the same segments of different species also vary in relative length and width. The specimens of *Hepialus humuli* and *Cossus cossus* used in this study are subequal in size, although the same segments are not similar in their relative length and width. Studying specimens so nearly equal in size, one's judgment of the corresponding positions of the setæ being considered is probably not far from the truth.

(a) The Prothorax.

Homologizing Cossus cossus with Hepialus humuli. The homology of setæ M, P, and L of *Cossus cossus* is very obvious, and only the remaining setæ, which are all dorsal in situation, need any discussion.

The number of setæ remaining is exactly the same on these two species and the number of punctures the same also, but the features of difference in the setal arrangement are great. They both have a cervical shield, but the size and shape of the cervical shield and the number of the setæ on it are very different. Therefore,

the cervical shield can not be used to any great extent as a fixed starting point in homologizing the setæ, but the setæ must be matched according to their corresponding positions, notwithstanding the great modifications which their positions have undergone.

The two punctures on the cervical shield of *Cossus cossus* are in a corresponding position with the punctures of *Hepialus humuli*; they are similar in position in both species. Owing to this similarity the punctures may serve as a landmark. Then the seta cephalo-ventrad of the dorsal puncture on the cervical shield of *Cossus cossus* should be A_1 , and the seta cephalo-ventrad of the other puncture and ventrad of A_1 should be A_2 , because such are the relations which the A_1 and A_2 of *Hepialus humuli* have with the punctures and with each other. Since the homology of A_1 and A_2 is determined, the remaining setæ can have their proper homology easily designated. One may doubt the value of the punctures, so this proof may be disregarded and a better one sought.

The most dorsal seta on the cervical shield of *Hepialus humuli* is D_1 . The most dorsal seta of *Cossus cossus* is similar to that of *Hepialus humuli* only in its relative distance from the dorso-mesal line but not from the cephalic margin of the cervical shield. Therefore only a partial proof has been offered for the homology of the most dorsal seta of *Cossus cossus*. If one disregards this partial proof and assumes this most dorsal seta of *Cossus cossus* to be D_2 , he must observe the relations of D_2 of *Hepialus humuli* with the other setæ and see if they agree with *Cossus cossus*. In *Hepialus humuli* D_2 is the most caudal seta and situated between A_1 and A_2 , i. e., the third seta counting from the dorso-mesal line. This particular seta of *Cossus cossus* under consideration fits neither of the above conditions. It is not the third seta counting from the dorso-mesal line, but the first, and it is too far cephalad to be in any way the most caudal seta. So it must be D_1 . In *Hepialus humuli* there is a cephalic row of five setæ. In *Cossus cossus* there is a cephalic row of four setæ. By the above evidences D_1 of *Cossus cossus* is not on the cephalic row. Therefore the four setæ of the cephalic row of *Cossus cossus* are homologous with A_1 , A_2 , S_2 and C_3 respectively, as they are very close in the corresponding positions. The most caudal seta and also the third seta from the

dorso-mesal line, caudad of A_1 of the cephalic row, is D_2 , because such is the relative position which D_2 of *Hepialus humuli* occupies. The single seta cephalo-ventrad of D_2 is S_1 , and the single seta ventrad of and almost dorso-ventrad in line with S_1 is C_1 , because they have the above conditions which the S_1 and the C_1 of *Hepialus humuli* have. The only remaining seta must be C_2 . It is not only for the reason that it is the only remaining seta, but also because it agrees with C_2 of *Hepialus humuli* in being the most ventral of the nine setæ.

Homologizing Other Species of Frenatæ with Cossus cossus.

The prothoracic setæ of *Archips cerasivorana*, *Trochilium apiformis* and *Pseudanaphora arcanella*, are very obviously homologous with the prothoracic setæ of *Cossus cossus*. Of course, they are not without variations. The variations of the position of L, P, and M are difficult to detect, so they are omitted from this discussion. The remaining setæ on the prothorax of the three species under consideration vary more or less in their positions, yet the remarkable coincidences of their relative positions are worthy of notice. D_1 never departs from being the most dorsal seta. D_2 never departs from the dorso-mesal line, and is always one of the caudal if not the most caudal seta. A_1 , A_2 , S_2 and C_3 always constitute the cephalic row of four setæ, although S_2 of *Trochilium apiformis* is a trifle caudad of the other three setæ, yet no one can deny its belonging to a cephalic row. C_2 never fails to be the most ventral seta of these nine setæ under consideration.

Of the Noctuidæ sketched in the setal maps the homology of the prothoracic setæ of *Heleophila unipuncta* and *Jaspedia celsia* may be noted. The homology of S_2 of *Jaspedia celsia* can be explained from the caudad gradations of S_2 of *Trochilium apiformis* and *Heleophila unipuncta*. The remaining two setæ are two of the C's. The difficulty is only that which two of the three C's are they and which C is lost? Judging from the facts that they are in corresponding positions with C_2 and C_3 on *Cossus cossus*, *Archips cerasivorana* and *Trochilium apiformis* and also from the fact that C_1 is the smallest of the three C's of *Cossus cossus*, these two setæ under consideration are determined to be C_2 and C_3 . Judging from the conditions on *Pseudanaphora arcanella*, the above decision may

be doubtful. From what we know about the adults, the former three species should rank, at least, in the same degree of generalization with the latter one. For the above reasons these two setæ on the Noctuidæ under consideration should be determined as C_2 and C_3 .

The homology of the prothoracic setæ of *Drepana falcataria* and *Polyphoca ridens* can be very easily determined by comparing them with the prothoracic setæ of the above species already discussed. After every seta of the species above discussed are homologized with the setæ on the prothorax of *Drepana falcataria* and of *Polyphoca ridens*, one can see that there are some setæ left unnamed. These setæ do not occur in any other species except the allies of the two species named. Since these setæ are found only on these species and their allies we may very safely conclude that these are examples of specialization by addition and the writer has therefore designated them as *ad*.

The spiny caterpillars, such as *Automeris io*, have their spines dendritically branched from the basal portions. That each basal portion represents a group, or groups, of setæ is very obvious. Their proper homology can be easily determined by comparing them with the setæ of the species already discussed above.

The hairy larva, *Isia isabella*, from the standpoint of homologizing its setæ is formidable looking indeed. Yet tracing from a well-stretched specimen it is found that the bases of the setæ are clustered on warts. The even surfaced hairy larva, *Zygæna trifolii*, has the setæ sufficiently isolated to enable the observer to differentiate them into clusters. Therefore, in all the hairy larvæ it is comparatively easy for one to determine the homology of their setæ. Of course, it is difficult to ascertain which is which within a group of setæ, but it is not difficult to separate them into groups. *Apetala hasta* furnishes a valuable key to the situation, as it is not specialized so much as some of the others and its primary setæ are readily distinguishable by their size.

(b) The Mesothorax and Metathorax.

In *Hepialus humuli* there is no striking difference in the setal arrangement of the mesothorax and metathorax. In all the Frenatæ studied only the position of A_{1a} varies very strikingly on

the metathorax and mesothorax of the same species. The further evidence for believing that the minute seta on the caudal margin of the cervical shield of larvæ of the Frenatæ studied is mesothoracic A_{1a} can be found in the larva of *Pseudanaphora arcanella*. The cervical shield of this species has a transverse ridge near its caudal margin. Behind the ridge is a suture-like depression. The larval skin is so unevenly chitinized and the cervical shield is so extended caudad that one can very naturally say that this suture is the separating line between the prothorax and the mesothorax. Therefore, mesothoracic A_{1a} being far caudad of this suture is naturally considered as belonging to the mesothorax.

Homologizing Cossus cossus with Hepialus humuli. The homology of M, P, and L of these two species is very obvious. A_1 and A_2 of the mesothorax of *Hepialus humuli* are on a wart, but the corresponding setæ are not on a wart on the metathorax. Therefore, these four minute setæ should be considered as four separate primary setæ and not as a single primary seta becoming tufted. Since they are like the four minute setæ of *Cossus cossus* in form and correspond with the latter in position, they must be homologous with the four minute setæ of *Cossus cossus* which are scattered in two pairs at an anterior position as A_1 and A_2 .

Since the homology of the above setæ is determined, the only setæ left are seven setæ in both *Hepialus humuli* and *Cossus cossus*. The seven setæ have their resemblance only in number in both of these species. Their arrangement is entirely different. If one assumes that the setæ migrate only to a very limited extent, it might be said that the divergent arrangement of the setæ occurring in these two species can not possibly be derived from a common ancestral form with only seven setæ, which they possess at present. According to this assumption the ancestral form should have ten setæ at least, and the assumed three additional setæ should be transversely in a row at the middle of the segment. The phrase "at least" is used because none of these two types of seta arrangement could be derived from this assumed type without some modifications. The seven setæ concerned in these two species show no difference even in size, and there is no structural evidence on the integument showing any evidence to prove the above assumption. Furthermore,

how can anyone know the extent of the migration of setæ taking place in these two species of two separate suborders? The contention of this paper is that it is probably much safer and nearer the truth to sort out some points of similarity from this greatly modified setal arrangement for the basis of homologizing these setæ instead of prooflessly assuming a number of setæ which do not actually exist.

The most dorsal seta of *Cossus cossus* agrees with D_1 of *Hepialus humuli* in its distance from the dorso-mesal line, but disagrees in the fact that it is situated at about the middle of the segment, while D_1 of *Hepialus humuli* is situated on the cephalic one-third of the segment. Then, can this most dorsal seta be homologous with D_2 of *Hepialus humuli*? No, it is not possible, because D_2 of *Hepialus humuli* is situated at the caudal one-third of the segment and is too far ventrad from the dorso-mesal line to be homologized with the most dorsal seta of *Cossus cossus*. Therefore, if the most dorsal seta of *Cossus cossus* can be homologized with any seta of *Hepialus humuli* at all, it must be D_1 and nothing else. The seta immediately ventrad of and in line with the most dorsal seta of *Cossus cossus* is D_2 and the seta still ventrad is S_1 . The seta ventrad of and in line with S_1 of *Cossus cossus* is considered to be S_2 , because S_2 of *Hepialus humuli* can not be homologous with the most ventral seta of these seven setæ concerned on *Cossus cossus* without a considerable ventral migration. This ventral migration is not less than the distance of the caudal migration, if S_2 of *Hepialus humuli* is homologous with the seta ventrad of and in line with S_1 of *Cossus cossus*. Since S_2 of *Hepialus humuli* is transversally in line with D_1 of the same species, S_1 of *Hepialus humuli* is more likely to be homologized with the seta ventrad of and in line with S_1 of *Cossus cossus* (i e., also in line with D_1) than with the most ventral seta of these seven setæ under consideration on *Cossus cossus*. The homology of C_1 of *Cossus cossus* can also be explained by this prevailing caudal migration of setæ. The homology of C_2 and C_3 , as shown in this section, will contradict the results of the study of the same larvæ unless the group C is definitely proved to be a natural group of

setæ having their constituents always occupying the same relative triangular position.

Even if the bar-like chitinized scar near C_3 of *Hepialus humuli* is assumed as an atrophied seta, thus absolutely disregarding its impossibility of being such, the situation will not be bettered, because this bar-like scar is not in any way in the corresponding position of any seta of *Cossus cossus*. Further, this assumption necessitates that we disregard the fact that the setæ of *Hepialus humuli* are equal in number and similar in relative size with the setæ of *Cossus cossus*.

Homologizing Other Species of Frenatæ with Cossus cossus. All the single-haired larvæ of Frenatæ have their mesothoracic and metathoracic setal arrangement like the type of *Cossus cossus*. The positions of the different setæ are always isolated enough so that they can be divided into groups; as A, D, S, C, L, P and M. In the case of *Drepana* and *Polyphoca* the extra setæ are known to be the additional ones by comparing them with the different species. The setæ of L vary in number in a few species; as two in *Archips cerasivorana* and four in *Drepana falcataria*. The hairy and spiny caterpillars can very easily have their clusters of setæ of spines homologized and designated with the same of the groups of setæ.

(c) The First Eight Abdominal Segments.

Although every one of the first eight abdominal segments of every individual larva has its own peculiarity regarding its setal arrangement, yet no one will have any difficulty in homologizing the setæ of any one of the first eight abdominal segments one with another. Therefore, the discussion of any one of the first eight abdominal segments of a species can be regarded as a representative discussion of all the remaining seven segments of the same species. The segment selected for the discussion in this passage and for the illustration in the setal map is the third abdominal segment.

Homologizing Cossus cossus with Hepialus humuli. D_1 , D_2 , S_2 , C_1 and M of the third abdominal segment of *Cossus cossus* and *Hepialus humuli* are exactly in the corresponding position. Therefore, their homology is very obvious. Since the homology of D_1 , D_2 , S_2 , and C_1 of *Cossus cossus* has been determined, then the

absence of S_1 on the third abdominal segment of *Cossus cossus* is evident. A of *Cossus cossus* consists of two minute setæ, while A of *Hepialus humuli* consists of only a single minute seta. P of *Cossus cossus* and of *Hepialus humuli* are of an equal number of four setæ; but P_4 of *Cossus cossus* is not on the proleg as is the case in P_4 of *Hepialus humuli*. In spite of the above differences A and P of these two species can be satisfactorily proved to be homologous by considering their relative size and position in comparing them with each other and also respectively with other setæ on each of the segments concerned. The remaining setæ of the third abdominal segment of these two species are all of an equal number of three setæ. If any seta or every one of these three setæ of one species can find any homologous seta on another species at all, the latter can be nothing else but one of these three remaining setæ, because the other setæ have their homology already precisely determined. The three remaining setæ of the third abdominal segment of *Hepialus humuli* are designated as C_2 , C_3 and L. L of *Hepialus humuli* is homologous with the most ventral seta of the remaining setæ of *Cossus cossus*, because the former corresponds more nearly with the latter in position. Thus the most ventral seta of the three remaining setæ of *Cossus cossus* is determined to be homologous with L of *Hepialus humuli* by means of the eliminative method. Even if the eliminative method is not employed and the homology of this particular seta of *Cossus cossus* (just determined as L) is first considered, this particular seta of *Cossus cossus* should be homologous with L of *Hepialus humuli*, because the former is the nearest like the latter in every aspect, the position it occupies and its relation with other structures. C_2 and C_3 of *Hepialus humuli* can not be in the position of the still remaining two setæ of *Cossus cossus* without a considerable migration. This migration may be a cephalo-ventral or a rotating one. There is no evidence, from the external study at least, to determine the route of migration which these setæ have followed. Therefore, these two still remaining setæ of *Cossus cossus* can be nothing but C_2 and C_3 , but it is difficult to determine which one of these two setæ is C_2 and which C_3 from this study.

Homologizing Other Frenatae with Cossus cossus. With the exception of the group of setæ C all the setæ of the third abdominal segment of *Trochilium*, *Archips*, *Pseudanaphora*, *Jaspedia* and *Heleophila* are very easily to be homologized with the setæ of the third abdominal segment of *Cossus cossus*. C_1 is very evidently absent on the third abdominal segment of *Archips*, *Trochilium* and *Pseudanaphora*. The absence of C_1 on the third abdominal segment of *Jaspedia* and *Heleophila* can be explained in two ways: First, there is a gradual separation of C_2 and C_3 which can be observed by comparing *Cossus*, *Archips*, *Trochilium*, and *Pseudanaphora*. The change from the position of C_2 of *Pseudanaphora* to the position of the seta caudad of the third abdominal spiracle of *Jaspedia* and *Heleophila* is not a great one. Second, C_1 of the first abdominal segments of *Cossus cossus* is never ventrad of the dorsal margin of the spiracle, while the seta caudad of the third abdominal spiracle of *Jaspedia* and *Heleophila* has its homologous seta of the same species far ventrad of the ventral margin of the seventh abdominal spiracle and never much dorsad of any of the abdominal spiracles. *Polyploca* and *Drepana* can be determined to have additional setæ by comparing them with the larvæ of Noctuidæ. The homology of the setæ of hairy and spiny larvæ can be determined by comparing them with the other Frenatae the homology of whose setæ has already been determined.

(d) **The Ninth Abdominal Segment.**

Owing to the limitation of time, only the three species which have been treated in the "study of the different segments of the same larvæ" will be treated here. The ninth abdominal setæ of *Cossus cossus* and the ninth abdominal setæ of *Hepialus humuli* can be very easily homologized by starting from the ventral side. Of course, one may start from any corresponding portion on the ninth abdominal segment of these two species concerned; but it is believed that the easiest way is to start from the ventral side, next to the easiest from the dorsal side, and the hardest from any portion of the segment between the ventral and dorsal sides. The homology of D_1 of *Cossus* can be determined by its relation with A_1 . The absence of S_1 of *Cossus cossus* is obvious from the fact

that S_1 of *Hepialus humuli* is very vestigial in form and corresponds to no seta of *Cossus cossus* in position.

Jaspedia differs from *Cossus* only in the absence of C_1 and P_2 among the setæ of the ninth abdominal segment. The reasons for believing them absent have been stated in the section treating of the different segments of the same larvæ and do not require further discussion here.

(e) The Anal Segment.

All the specimens of larvæ had their anal segments more or less torn. Owing to this difficulty no setal map of the anal segment is made. It is judged from observations that, as far as the setal arrangement is concerned, the anal segment consists of more than a single segment.

From the above representations one can see that it is much easier to homologize the setæ of the same segments of different larvæ of the suborder Frenatæ with another larva of the same suborder than with that of the different suborder Jugatæ. From the experience of homologizing the setæ of the same segments of different larvæ, especially the thoracic segments of *Hepialus humuli* and of *Cossus cossus*, it is found much easier to start from the mesal line. A number of setæ of the thoracic segments of *Hepialus humuli* are separated from each other and are scattered, some cephalad and some caudad, on the segment, but practically no setæ are situated exactly midway between the cephalic and caudal limits of the segment, while a number of the setæ of the thoracic segments of *Cossus cossus* are arranged almost transversally in line with each other and midway between the cephalic and caudal limits of the segment. Therefore, the only means of homologizing the setæ on the same segments of these two species is to rely upon the distance of the setæ from the dorso-mesal line of the respective segments. Furthermore, one can not put the same segments of two different larvæ end to end for comparison. To find the corresponding position of one setæ of one larva with regard to another seta of another larva, the farther the seta departs from the mesal line the more difficult it is, because the curvature of the body and the presence of the other setæ will all act as an interference in ascertaining the corresponding distances of the setæ from the mesal line. For these reasons it has been found that in homologizing the setæ of *Hepialus* with the setæ of *Cossus*, one will obtain the results more easily and more accurately by starting from the mesal line.

IV. GENERAL DISCUSSION.

The presentations of the two preceding sections are of a very limited character. There are a number of points which can not be

discussed within their limits. In order to discuss these miscellaneous points for formulating a general discussion, all the restrictions which have been made for the two preceding sections will not be observed in this section.

(a) **The Results of the Study of the Same and Different Segments of the Larvæ.**

The results obtained from both the studies of the same and different segments are generally in harmony with each other. Not only this, but the unascertained points of one study may be ascertained by the results of the other study. These points will be discussed in two ways: to consider each segment as a whole, and to consider each single seta or each group of setæ.

Considering Each Segment as a Whole. Although the evidences offered for the homology of the mesothoracic and metathoracic setæ of *Cossus cossus* and of *Hepialus humuli* are the most probable ones, yet they are not very satisfactory as a whole. The homology of the prothoracic and abdominal setæ of *Cossus* and of *Hepialus* has been satisfactorily proved. And also the setæ on every body segment of *Cossus cossus* has been proved to be serially homologous. Therefore, it is not entirely assumption to say that every mesothoracic and methoracic seta of *Cossus cossus* finds its homologous seta on the mesothorax and metathorax of *Hepialus humuli*. Since the above point is clear, the bar-like scar of *Hepialus humuli* can not be considered as a seta under any circumstances.

Considering a Single Seta or a Group of Setæ. The doubt of the homology of A_1 and of A_2 of the prothorax of *Hepialus* can be removed by studying any frenate larva. The reason that A of an abdominal segment is only one minute seta in *Hepialus humuli* but two in *Cossus cossus*, can be sought from the study of the thoracic segments of the two species concerned. The absence of C_1 on the abdominal segments of *Jaspedia* and others has already been precisely stated.

(b) **The Value of Other Structures and the Sizes of Setæ.**

In the introductory section of this paper on the homology of the body setæ of lepidopterous larvæ, a number of difficulties have been stated. Several points may not appear to be conclusive. Some of the following isolated discussions will confirm the statements

made in the introductory section and will also show that the difficulties hinted at in the sections on the preliminary considerations are not the only difficulties in homologizing the setæ of lepidopterous larvæ.

Punctures of the Prothorax. The homology of the two punctures on the cervical shield of the prothorax of *Cossus* and *Hepialus* has not been discussed by previous authors. The puncture is round and is identical in appearance with the base of a seta. The main difference between a seta and a puncture on the cervical shield is that the latter has not the shaft of a seta. As far as the writer's observations of the prothoracic segments of *Hepialus*, *Cossus*, *Trochilium*, *Archips*, *Jaspedia*, *Heleophila* and a number of Noctuidæ are concerned, the punctures are always two in number and in the same relative position in every species. There are no setæ but punctures on the cervical shield of *Tischeria malifoliella*, each puncture of this species takes the definite position of a seta on the cervical shield. It is for these reasons that the position of the punctures has been employed as one of the evidences of the homology of the prothoracic setæ of *Hepialus humuli* and of *Cossus cossus*. From the above facts, it may not be assuming even to designate these two punctures as A_{1b} and A_{2b} respectively. This paper has not homologized the punctures on the cervical shield with any seta at all. The reasons are that there is no paper to the writer's knowledge in which is discussed the morphology of the punctures, and the writer has not had an opportunity to make a histological study of them. This is the reason that the position of the punctures has been disregarded as an evidence in homologizing the prothoracic setæ, and is also the reason that the position of the punctures is usually not indicated on the setal map.

The Thoracic Legs. The thoracic legs differ from the prolegs in a number of ways. First, the thoracic leg has a suture at its base separating it from the general integument, while the proleg has not such a suture. Second, the thoracic leg is segmented, while the proleg is not. Third, the setæ of the thoracic legs are not homologous with the body setæ, while the setæ of the prolegs are homologous with those of the body. Fourth, as far as the setæ are concerned, the thoracic legs are true legs, while the prolegs,

provided with hooks at their apices, are only expanded portions of the integument bearing body setæ.

The Strongly Chitinized Portion of the Integument. It is not the purpose of this paper to discuss the origin of the strongly chitinized portion of the integument. But as far as the homology of the body setæ is concerned, the strongly chitinized portion of the integument of the body segments of lepidopterous larvæ has no more value than the pigments of the larval body. For instance, *Hepialus lecta* has its mesothoracic D_2 , S_1 , C_1 , and C_2 on a common large chitinized portion of the integument, while *Hepialus humuli* has its mesothoracic D_2 , S_1 , C_1 , and C_2 not on a common chitinized portion of the integument but each of these four setæ is either on a separate small portion of the integument or is without a chitinized portion of integument at the base. Since the homology of the setæ of these two species of the same genus, *Hepialus*, is beyond any doubt, then what can be the value of the strongly chitinized portions of the integument of the lepidopterous larval body segments? The above is not the only instance, many similar examples could be cited. This is the reason why the position of the strongly chitinized portion of the integument is not always indicated on the setal map. And it is for this reason that the phrase "strongly chitinized portion of the integument" is employed in this paper instead of "chitinized plate," as the word "plate" gives the conception of a morphological unit. Even the term "cervical shield," the largest strongly chitinized portion of the integument, is of too doubtful a structure to be a morphological unit. The limits of the extensions of the cervical shield, the ventral extensions at least, are not marked by a suture. Among species of the genus *Mamestra* certain of them have a cervical shield and some not. Comparing the prothorax of *Hepialus*, *Cossus*, *Jaspedia*, and *Heleophila*, one fails to see any constancy in the structure of the cervical shield. The term "cervical shield" employed in this paper is simply the adoption of an old terminology for the convenience of description.

The "Annulets" of the Body Segments. The so-called "annulets" of the body segment of lepidopterous larvæ are bounded by the transverse wrinkles of the body segments. The wrinkles are not sutures, nor are they well defined. Furthermore, if the "annu-

let" has any value at all, the mesothoracic setæ can never be homologous with the setæ on the cervical shield of the prothorax in any way, as the mesothorax is apparently divided into three or four annulets, while the cervical shield is a solid piece in appearance in most species. Therefore, the term "annulet" can not be considered under any circumstance as a morphological unit, nor even as a practical term, for the wrinkles disappear when the larva is well stretched.

The size of the Setæ. The relative size of the setæ has been very frequently offered as evidence for homologizing the setæ, but the absolute size of the setæ has never been considered in this paper. If the absolute size of the setæ is considered, P of the thoracic segments can not be homologous with P of the abdominal segments. A of prothorax can not be homologous with A of other segments. Since the homology of these two groups of setæ of all the body segments is evident, then the absolute size of the setæ would be misleading for the determination of the homology.

(c) Discussion of Papers of Previous Authors.

The body setæ of lepidopterous larvæ have been considered by numerous authors. But there are only a very few authors who have named individual setæ. The homology here proposed differs to a very large extent from previous authors. This passage does not intend to discuss every point of controversy. The discussion is divided into two topics: the "unexplained" setæ and the "sub-primary" setæ.

The Unexplained Setæ. "On the thorax (of *Hepialus humuli*) the upper anterior primary seta (D_1) is unexplained.*" This quotation refers probably to the mesothorax and metathorax, as the prothoracic setæ have not been dwelt on at length by previous authors. If D_1 of the mesothorax and metathorax of *Hepialus* is "unexplainable" on account of its cephalic position, then D_2 of the mesothorax and metathorax of *Hepialus* should be also unexplainable on account of their caudal position. The same author has said that "It is true that considerable movements may occur." Since the movement of the setæ is granted as possible, then one can not make a rule that certain setæ are allowed to move from a

*[Dyar, H. G. (1895), Am. Naturalist, Vol. 29, p. 1068.]

caudal position to the middle while certain setæ are not allowed to move from a cephalic position to the middle of a segment.

The Subprimary Setæ. Certain setæ are said not to appear during the first larval instar and have been termed the "Subprimary" setæ by previous authors. This terminology is, however, very doubtful. First, certain setæ very minute in size, such as A of *Cossus cossus*, of all the segments except the prothorax has not been observed by previous authors. May not these subprimary setæ disappear only in the observer's vision? Second, Thomas Montgomery (1906) in his book on "The Analysis of Racial Descent in Animals" cited a number of embryological records showing that the precisely homologous organs of different species of a genus arise in very different embryonic stages. A statement of Montgomery (p. 240) may be quoted as follows: "For these reasons the relative time of succession of organs in the ontogeny is regarded as a character of conservation. It does not present a criterion of homology, but one of relative stability. This is not to be interpreted to mean that organs are to be rated strictly according to their embryonic succession....." Third, are the different kinds of eyes of adult insects having complete and incomplete and no metamorphosis homologous? It would certainly be very odd to distinguish the adult insect eyes as "primary" and "subprimary." It is for these reasons that the distinction of "subprimary setæ" is not considered in this paper.

From a study of 170 species of lepidopterous larvæ, very largely Noctuidæ, the division of setæ into groups may be briefly considered. The groups of setæ dorsal (D), latero-ventral (L), pseudopodal (P), midventral (M) and anterior (A) can be very easily recognized as groups. The subdorsal group (S) of *Hepialus* may not be considered by some as a distinctly separate group of setæ. Yet a straight line drawn between them connects S_1 and S_2 of *Hepialus* and does not pass through any seta between S_1 and S_2 , and S is a very prominent group of the frenate larvæ. With the exception of C_1 of the first abdominal segments of *Cossus cossus*, which is nearer to S_2 than to its fellows, the circumstigmatal group

(C) of setæ is always a very distinguishable group on every segment of larvæ that has been examined.

From the practical point of view there are a number of setæ whose homology can not be determined without dividing the setæ into groups. First, every cluster of setæ on the hairy or spiny caterpillars represents usually more than one primary seta. From a study of the body of *Apetala hasta*, one may be able to tell precisely how many primary setæ every cluster of setæ represents. If a cluster of setæ of one larva should occupy the corresponding position of a single primary seta of another larva, the former must certainly be homologous with the latter. If a cluster of setæ of one larva occupies the corresponding position of a group of primary setæ of another larva, the former may represent a group of setæ or only a part of the group of setæ as the prothoracic C (=Forbes' prespiracular tubercle). This name is not adopted in this paper because Forbes applies it only to the prothorax of frenate larvæ. To designate such a cluster of setæ with the name of a group of setæ is not precise, but it is easier for reaching the truth to ascertain what are the primary setæ represented in such a cluster of setæ. Second, in the case of a larva where the setæ are single, this grouping system is also very useful. A, the anterior group of setæ, has its number of setæ varying from one to four. L, the latero-ventral group of setæ, has usually two setæ on the prothorax and one seta on other segments, but L of *Archips cerasivorana* and *Glottula pancratii* has two setæ on the mesothorax and metathorax. S of prothorax usually consists of two setæ but it consists of only one seta on the prothorax of *Simplicia rectalis*. In homologizing the setæ of the examples given above, it would be impossible to determine the homology of individual setæ. Furthermore, the position occupied by each group of setæ on the body segment of any larva is not always very much diversified from the position or the name of the group of setæ indicated.

V. SUMMARY OF CONCLUSIONS.

1. The only reliable means of ascertaining the homology of the body setæ of lepidopterous larvæ is to associate the corresponding positions which the setæ occupy.

2. The setæ of any body segment of a lepidopterous larva are homologous both with the setæ of every other segment of the same larva and with the setæ of the same segment of different larvæ.

3. The setæ may be increased in number and reduced in number as the results of specialization.

4. The thoracic setæ of the larvæ of the suborder Jugatæ do not differ from the thoracic setæ of the larvæ of generalized Frenatæ in number, but do differ in arrangement of certain groups of setæ.

5. *Cossus cossus* can be considered as the most generalized of the Frenatæ from the fact that it has no additional setæ and retains C_1 on all the abdominal segments and on the prothorax, while other Frenatæ do not retain this seta.

6. The abdomen of lepidopterous larvæ consists of more than ten segments.

7. The setæ of the prothorax differ from the setæ of the mesothorax and metathorax, but they are more similar to the latter than to the setæ of any abdominal segment, and *vice versa*.

8. The thoracic segments are more generalized than the abdominal segments.

9. The setæ can be divided into groups; the homology of each group of setæ is much more evident than the homology of the individual seta within a group.

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EXPLANATION OF PLATES.

The position of the setæ is indicated by a small dot. The shaft of the seta is not indicated. The letters used for the setæ explained in the text (p. 7). Other abbreviations used in the plates are: *sp*=spiracles; *p*=punctures; and *meso* $A_{1a}=A_{1a}$ of the mesothorax.

Plate X

Fig. 1. Setal maps of *Hepialus humuli* L.

Fig. 2. Setal maps of *Cossus cossus* L.

Fig. 3. Setal maps of *Jaspedia celsia* L.

a, Prothorax; *b*, Mesothorax; *c*, Metathorax; *d*, First abdominal segment; *e*, Eighth abdominal segment; *f*, Ninth abdominal segment.

Plate XI

Fig. 1. Setal maps of prothorax.

Fig. 2. Setal maps of metathorax.

Fig. 3. Setal maps of third abdominal segment.

a, *Hepialus humuli* L; *b*, *Cossus cossus* L; *c*, *Archips cerasivorana* Fitch; *d*, *Trochilium apiformis* Clemens; *e*, *Pseudanaphora aranella* Clemens.

Plate XII

Fig. 1. Setal maps of prothorax.

Fig. 2. Setal maps of metathorax.

Fig. 3. Setal maps of third abdominal segment.

a, *Heliophila unipuncta* Haworth; *b*, *Jaspedia celsia* L; *c*, *Drepana falcataria* L; *d*, *Polyploca ridens* F; *e*, *Apatela hasta* Guenée.

Plate XIII

Fig. 1. Setal maps of prothorax.

Fig. 2. Setal maps of metathorax.

Fig. 3. Setal maps of third abdominal segment.

a, *Apatela oblinita* Smith and Abbott; *b*, *Automeris io* Fabricius; *c*, *Nola cucullatella* L; *d*, *Zygæna trifolii* Esp; *e*, *Isia isabella* Smith and Abbott.

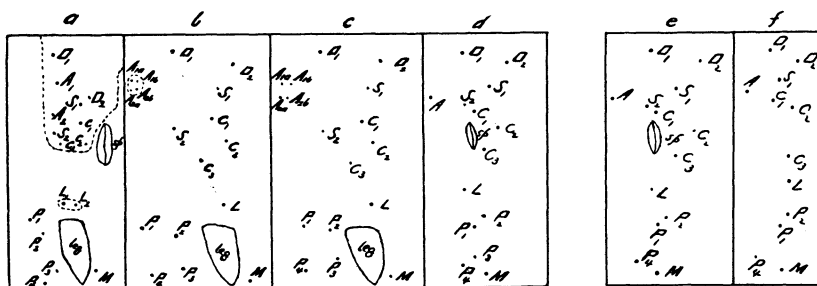


Fig. 1

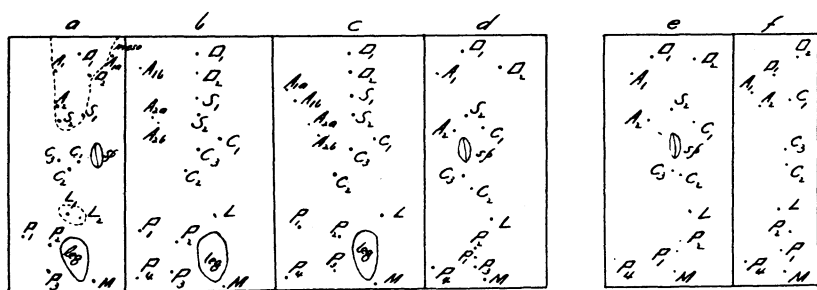


Fig. 2

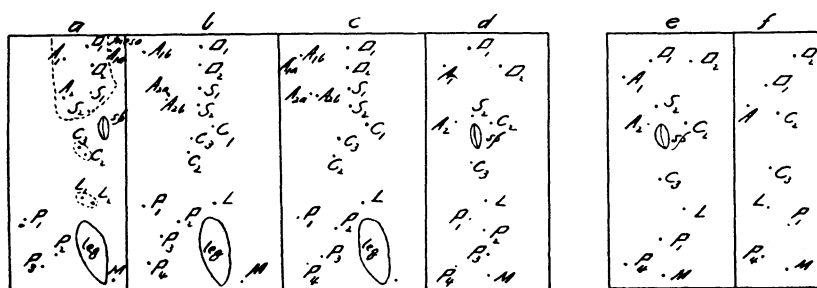


Fig. 3

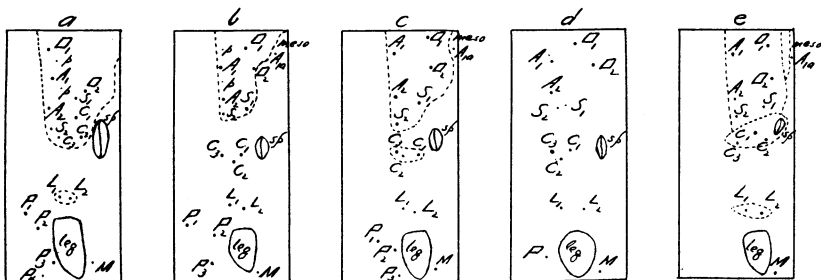


Fig 1

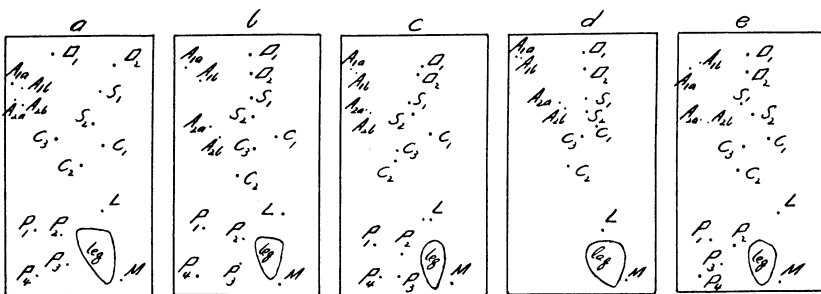


Fig 2

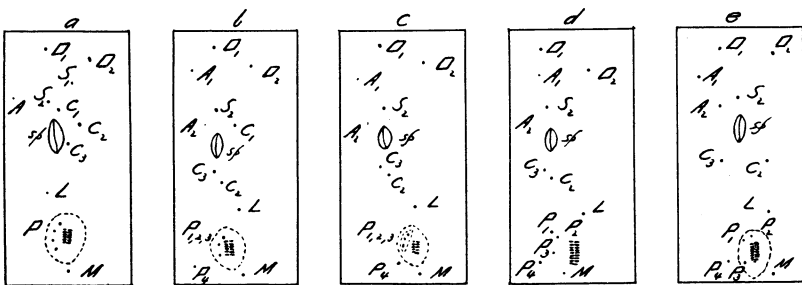


Fig 3

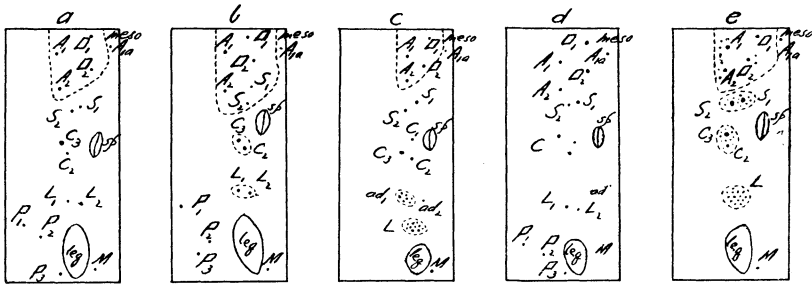


Fig 1

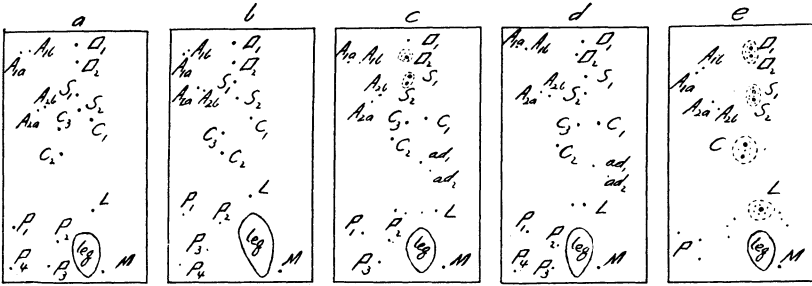


Fig 2

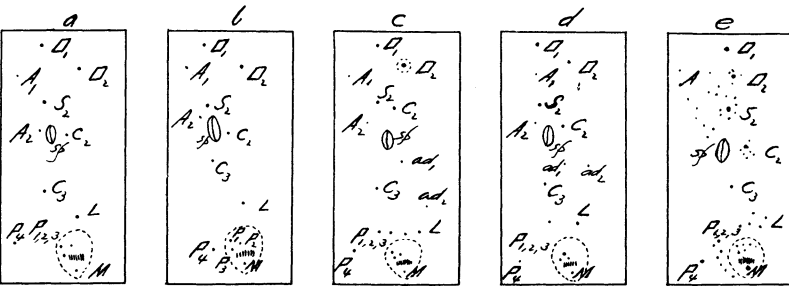


Fig 3

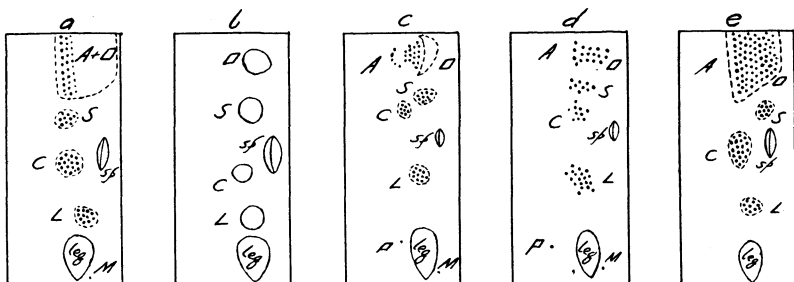


Fig. 1

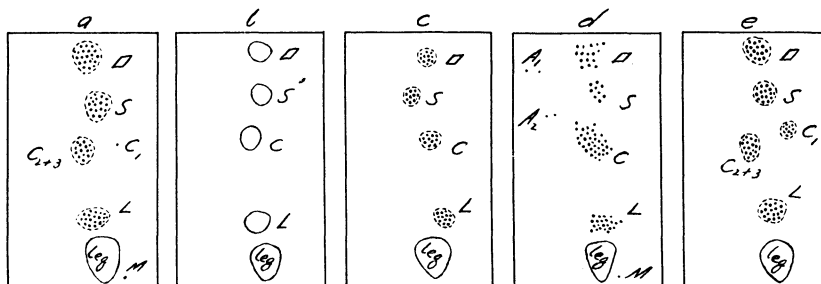


Fig. 2

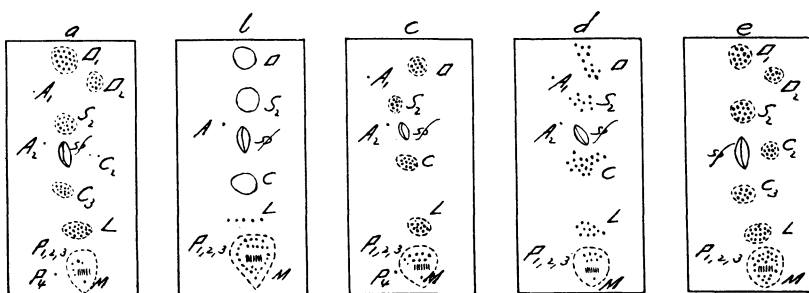


Fig. 3